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Intentional Switches Between Bimanual Coordination Patterns Are Primarily Effectuated by the Nondominant Hand

Harjo J. de Poel, C. (Lieke) E. Peper, and Peter J. Beek

Based on indications that hand dominance is characterized by asymmetrical interlimb coupling strength (with the dominant hand exerting stronger influences on the nondominant hand than vice versa), intentional switches between rhythmic bimanual coordination patterns were predicted to be mediated primarily by phase adaptations in the movements of the nondominant hand. This hypothesis was supported for both right-handed and left-handed participants who performed voluntary switches from in-phase to antiphase coordination and vice versa, at four different frequencies. In accordance with previous indications that handedness is expressed less consistently in left-handers, the asymmetry between the hands was less pronounced in left-handed than in right-handed participants. The asymmetry was smaller for switches from in-phase to antiphase coordination (i.e., in the direction opposite to spontaneous transitions) than for switches in the reverse direction, suggesting that (the expression of) the handedness-related asymmetry in coupling strength was weakened by intentional processes associated with these switches.

Key Words: handedness, interlimb interactions, asymmetric coupling, coordination dynamics, rhythmic movement

Rhythmic interlimb coordination is characterized by attraction to a limited number of frequency and phase relations (Peper, Beek, & Van Wieringen, 1995; Tuller & Kelso, 1989; Yamanishi, Kawato, & Suzuki, 1980; Zanone & Kelso, 1992), which owe their stability to (mutual) interactions between the participating limbs. For isofrequency coordination, the empirically observed stability properties have been accounted for in terms of a dynamical model of coupled oscillators, commonly referred to as the HKB model (Haken, Kelso, & Bunz, 1985). Although the interactions between the limbs were originally modeled by means of a symmetric coupling between the associated oscillators, converging evidence indicates that the strength of coupling between the upper limbs is asymmetric as a function of hand dominance. This implies that the effects of handedness are not limited to the quality of unimanual task performance (e.g., Bagesteiro & Sainburg, 2002; Peters, 1980;

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Sainburg, 2002) and a preference for assigning manipulative roles to the dominant hand and stabilizing roles to the nondominant hand (cf. Guiard, 1987; Peters, 1994), but extend to the degree to which the limbs influence each other in bimanual tasks consisting of two identical subtasks (i.e., oscillation at a common frequency).

The assertion that hand dominance is associated with an asymmetry in the degree to which the upper limbs influence each other is based on both theoretical and empirical—neurophysiological and behavioral—evidence. On the theoretical side, the subtle, yet systematic effects of handedness on the relative phase dynamics (e.g., shifts in mean relative phasing), were captured by adding additional symmetry-breaking sine terms to the original (symmetric) HKB potential (Treffner & Turvey, 1995, 1996). Peper, Daffertshofer, and Beek (2004) recently demonstrated that this asymmetric potential and, thus, the associated handedness-related coordination phenomena, can be formally understood in terms of an asymmetry in the strength of the coupling between the oscillating limbs, with the dominant limb exerting a stronger influence on the nondominant limb than vice versa (see also De Poel, Peper & Beek, 2005; for related suggestions, see Carson, 1993).

This interpretation is consistent with neurophysiological findings regarding candidate sources of interlimb interactions. For instance, interlimb coupling effects might ensue from uncrossed corticospinal pathways (cf. Carson, 2005; Cattaert, Semjen, & Summers, 1999). Recent TMS studies examining the influence of these uncrossed pathways on muscle activation in the ipsilateral limb indicated that the nondominant (left) limb was more strongly influenced by brain activity associated with the dominant (right) limb than vice versa (Kagerer, Summers, & Semjen, 2003). In addition, short-interval bilateral TMS studies revealed stronger inhibitory influences from the dominant onto the nondominant hemisphere than in the reverse direction (Kobayashi, Hutchinson, Schlaug, & Pascual-Leone, 2003; Netz, Ziemann, & Homburg, 1995; Stinear & Byblow, 2004). This finding is consistent with the suggestion that the dominant hemisphere is more efficient in inhibiting the hemispheric drive stemming from the nondominant side than vice versa (Serrien, Cassidy, & Brown, 2003), which is in accordance with the suggested asymmetry in interlimb coupling strength.

Finally, there is considerable behavioral evidence for a handedness-related asymmetry in coupling strength. A frequently addressed phenomenon in isofrequency coordination is the spontaneous transition from antiphase (originally defined as alternating activation of homologous muscles; relative phase $\phi = 180^\circ$) to in-phase coordination (simultaneous activation of homologous muscles; $\phi = 0^\circ$) that occurs when movement tempo is gradually increased (Kelso, 1984). During such a transition at least one of the limbs has to change its phasing so that the new phase relation is attained. De Poel et al. (2005) recently demonstrated that in both left-handed (LH) and right-handed (RH) participants the associated phase adaptations were larger in the nondominant hand than in the dominant hand, although the difference between the hands in this regard was larger for RH than for LH participants (for whom the difference did not reach significance). This result was consistent with previous observations obtained for RH individuals (Byblow, Carson, & Goodman, 1994; Byblow, Chua, & Goodman, 1995). Similarly, transitions from asymmetric to symmetric bimanual circle drawing have been shown to be mainly mediated by a change in movement direction of the nondominant hand (Byblow, Chua, Bysouth-Young, & Summers, 1999; Carson, Thomas, Summers, Walters, & Semjen, 1997; Wuyts,

Summers, Carson, Byblow, & Semjen, 1996). Because the transient stage during such spontaneous transitions is governed by the stability properties that result from the interactions between the limbs, the observed predominance of adaptations in the phasing of the nondominant limb is consistent with the postulated asymmetry in interlimb coupling strength. This interpretation was further underscored by the characteristics of the relaxation process in response to an external perturbation of the interlimb coordination pattern. The restabilization of the original coordination pattern appeared to be mediated primarily by phase adaptations in the nondominant limb, reflecting the proposed asymmetry in interlimb coupling strength (De Poel et al., 2005). Although this effect was observed for both LH and RH participants, it was more pronounced for the RH group.

In sum, theoretical considerations in combination with recent neurophysiological findings regarding the effects of hand dominance onto interlimb coupling strength are consistent with the behavioral characteristics observed during transient stages that are governed by the stability features of rhythmic interlimb coordination. Another form of transient behavior is observed when voluntary switches between coordination patterns are performed. Although in this situation the changes in relative phasing do not follow from the ("intrinsic") coordinative stability properties, several studies have demonstrated that the quickness of such switches (i.e., the switching time) depends on the stability of the coordination patterns involved. In particular, switches from patterns with lower stability (e.g., antiphase) to patterns with higher stability (e.g., in-phase) are typically performed faster than switches in the reverse direction (Byblow, Lewis, Stinear, Austin, & Lynch, 2000; Carson, Byblow, Abernethy, & Summers, 1996; Serrien & Swinnen, 1999; Kelso, Scholz, & Schöner, 1988; Scholz & Kelso, 1990), which is consistent with the theoretical predictions formulated by Kelso et al. (1988; see also Scholz & Kelso, 1990). The observed influence of coordinative stability in this regard indicates that the performance of intentional switches is (partly) shaped by the interactions between the limbs, suggesting that the handedness-related asymmetry in coupling strength may affect the way in which the switches are effectuated.

Indeed, several results obtained for RH participants point in this direction. Whereas, for bimanual circle drawing, switching time was demonstrated to be independent of the hand that mediated the switch (Byblow, Summers, Semjen, Wuyts, & Carson, 1999; Wuyts, Byblow, Summers, Carson, & Semjen, 1998; but see also Byblow et al., 2000), switches that were (by instruction) mediated by the dominant hand resulted in larger disruptions in the movement pattern of the contralateral hand (reflecting interlimb interactions) than did switches mediated by the nondominant hand (Byblow et al., 1999, 2000). For bimanual coordination of rhythmic supination-pronation movements, Carson et al. (1996) found that in most cases switches from in-phase to antiphase coordination were mediated by the nondominant (left) hand. Verheul and Geuze (2004), on the other hand, argued that in their experiment (involving intentional switches between bimanual finger tapping patterns) the switching strategy primarily depended on the resulting change in relative phasing (viz., increasing or decreasing) rather than on the hand that mediated the phase change. They also reported, however, that switches mediated by slowing down the nondominant (left) hand occurred most often.

Together, these results obtained for RH participants suggest that the way in which intentional changes in rhythmic interlimb coordination are carried through

is influenced by hand dominance. Whereas, at first sight, one might expect that the dominant limb is used to mediate the voluntary change in interlimb phasing (given its more efficient control; cf. Bagesteiro & Sainburg, 2002; Sainburg, 2002), these studies indicated that the phase adaptations were predominantly made by the nondominant limb instead. Although these findings are consistent with the proposed asymmetry in interlimb coupling strength, with the nondominant limb being more strongly influenced (“attracted”) by the dominant limb than vice versa (e.g., Byblow et al., 2000; Carson, 1993; Peper et al., 2004; Treffner & Turvey, 1995, 1996), a thorough evaluation of the effects of hand dominance in this regard requires a systematic comparison of the performance of LH and RH individuals. Explicit examination of the differences between these two groups is important, because LH persons cannot be simply regarded as “inverted” RH persons. In the majority of LH individuals, hemispheric specialization corresponds to that observed in right-handers (e.g., language areas are located in the left hemisphere; Kandel, Schwartz, & Jessell, 1991), and handedness-related motor-cortical asymmetries have been reported to be more pronounced in RH than in LH individuals (Amunts et al., 1996; Kandel et al., 1991). In addition, there are many indications that left-handers are less consistent in their expression of hand dominance than right-handers (e.g., De Poel et al., 2005; McManus, Porac, Bryden, & Boucher, 1999; Peters & Servos, 1989; Shen & Franz, 2005), which could be associated with neurophysiological differences in lateralization or with the fact that left-handers have typically been raised in a “right-handed world” (McManus, 2002; Provins, 1997).

To test the hypothesis that intentional switches between coordination patterns were influenced by hand dominance, an experiment was conducted involving both RH and LH participants. In particular, it was predicted that, due to the handedness-related asymmetry in coupling strength, the transition would be primarily mediated by phase adaptations in the nondominant hand. In addition, these effects were predicted to be more pronounced for RH participants than for LH participants, in line with the results of De Poel et al. (2005).

Before turning to the experiment, it is useful to highlight some important differences between intentional switches and frequency-induced spontaneous transitions. The first difference concerns the direction of the switch. For spontaneous transitions the changes in relative phasing are directly dictated by the difference in coordinative stability between the two patterns, resulting in transitions from the less stable to the more stable pattern, whereas this difference does not constrain the direction of intentional switches. For isofrequency coordination, this implies that intentional switches from antiphase to in-phase as well as switches in the opposite direction can be examined. Previous results have indicated that voluntary switches in these two directions are performed in different ways (Byblow et al., 1999; Carson et al., 1996). In addition, it has been suggested that voluntary switches and spontaneous transitions might involve different neurophysiological processes (Byblow et al., 1999; 2000). Accordingly, the way in which hand dominance affects intentional switching behavior cannot be simply inferred from the characteristics of frequency-induced, spontaneous transitions in LH and RH participants (as obtained by De Poel et al., 2005).

Another striking difference is that, unlike frequency-induced spontaneous transitions, voluntary switches can be examined at various tempos of performance.

Higher movement frequencies have been shown to result in faster switches between coordination patterns (Carson et al., 1996; Scholz & Kelso, 1990). It is currently unclear, however, whether this frequency dependence of switching time is associated with variations in the degree to which the switch is mediated by either hand. Given recent indications that the asymmetry in coupling strength increases with movement frequency (De Poel et al., 2005), it might be expected that the handedness-related asymmetry between the hands (regarding their respective contributions to the switch) is larger when the patterns are performed at a higher tempo. This third prediction was also tested in the experiment.

The three predictions motivated in the preceding were examined by comparing how LH and RH participants performed intentional switches from the in-phase to the antiphase coordination pattern and vice versa. In particular, the analyses focused on the relative contributions of the individual hands in effectuating the intended change in interlimb phasing.

Methods

Participants

Fourteen volunteers (8 females and 6 males, age 18-24 years) were invited to participate in the experiment. They were selected on the basis of the experimenters' impression of their hand preference. Based on a Dutch version of the Edinburgh Handedness Inventory (Oldfield, 1971) the handedness quotient (or laterality quotient: LQ) was determined for each participant, with LQ = -100% indicating extreme left-handedness and LQ = +100% indicating extreme right-handedness. To preserve the naivety of the participants with respect to the purpose of the study, this handedness questionnaire was filled out after the experiment was completed. Participants with an LQ > 33% were labeled as RH, while participants with an LQ < -33% were labeled as LH. Seven participants were right-handed (mean LQ = 82%, range 47% to 100%), while six were left-handed (mean LQ = -88%, range -71% to -100%). One anticipated LH participant was excluded from the analyses because he turned out to be ambidextrous (LQ = -7%). The participants gave their informed consent prior to the experiment.

Apparatus

Participants were seated in a height-adjustable chair. The lower arms were placed on arm rests in a neutral position (thumbs up and hand palms facing inward) and their position was secured by the support surface on the medial and ventral side, by two adjustable vertical foam-coated rods on the dorsal side, and one adjustable horizontal foam-coated rod on the lateral side. Both hands were fixed against flat manipulanda by two straps, with all fingers extended. The manipulanda allowed for flexion-extension movements about the wrist in the horizontal plane only and were mounted on a vertical axis with a potentiometer at its lower end (Sakae, type FCP40A-5k, linearity 0.1%). The potentiometer's output voltage was digitized by a 12-bit ADC (Labmaster DMA) and stored on a microcomputer with a sampling frequency of 200 Hz. Computer-generated auditory pacing stimuli (pitch: 200 Hz, duration: 50 ms) were presented using headphones (Sennheiser HD 520 II). A green

light-emitting diode (LED; diameter: approximately 1.0 cm) positioned 1.5 m in front of the participant served as visual stimulus to trigger the intended switch in coordination.

Procedure

The participants performed bimanual oscillatory movements in either in-phase or antiphase coordination at four different frequencies that were specified by means of the auditory pacing signal. One pulse was presented for each half cycle of the movement. During in-phase coordination, participants were instructed to synchronize extension of both hands with a given beep and flexion with the next beep. In the antiphase mode, simultaneous flexion of one hand and extension of the other hand had to coincide with the pacing signal. Participants were instructed to start in either the in-phase or antiphase mode and to switch to the other mode when indicated to do so by the visual stimulus. To this end, the LED was turned on at a random moment between the fifth and the fifteenth cycle and remained illuminated for 3 s. The switch had to be performed in a fluent fashion within the illumination period, and it was emphasized that there was no need to react as fast as possible, since the task was not a reaction time task. The required movement frequencies were 1 Hz, 1.25 Hz, 1.5 Hz, and 1.75 Hz and trial length was 25 cycles in all conditions. The trials were grouped in two “switch condition blocks” (in-phase to antiphase and antiphase to in-phase), the order of which were counterbalanced over participants. Within each block, four “frequency blocks” were presented in random order. Each condition was repeated four times in a row. One familiarization trial for each condition preceded the 32 experimental trials.

All procedures adhered to the ethical guidelines of the American Psychological Association and were approved by the Ethics Committee of the Faculty of Human Movement Sciences of the Vrije Universiteit, Amsterdam.

Data Reduction

The angular position signals were low-pass filtered (bi-directional second-order Butterworth filter, cut-off frequency 10 Hz) and subsequently differentiated (five-point approximation) to obtain angular velocity. Inspection of the position data revealed unsystematic variations in the center of oscillation, especially during the switching period. Therefore, angular position was normalized to the associated amplitude for each half cycle, yielding a signal ranging from -1 to 1 . Equivalently, angular velocity was normalized to peak velocity for each half cycle. For both normalizations the onset and end of each half cycle were established by means of a custom-made peak-picking algorithm applied to the position data. The continuous phase angle (θ , in degrees) was determined for each hand, using $\theta_i = \tan^{-1}(\dot{x}_i^*/x_i^*)$, with x_i^* denoting normalized angular position, \dot{x}_i^* denoting normalized angular velocity, and i indicating the sample index. For each trial, the phase angles were “unwrapped” (i.e., summed over successive cycles), resulting in a progressively increasing phase angle per hand (i.e., θ_L and θ_R). The continuous relative phase between the hands (ϕ) was defined as $\phi = \theta_L - \theta_R$.

Analysis

Pre- and Post-Switch Performance

To relate the empirical results regarding the asymmetry in coupling strength to the previously identified coordination dynamics, steady-state behavior was analyzed. That is, the mean movement frequency of the right and left hand as well as the mean of ϕ ($\bar{\phi}$) and its standard deviation ($SD\phi$) were determined: for pre-switch performance (as obtained for the five cycles preceding the onset of the visual stimulus) and for post-switch performance (as obtained for the five cycles after the stimulus went off). This yielded two values (“pre” and “post”) per trial for each of these performance measures. The mean phase shift ($\Delta\phi_j$, with j denoting “pre” or “post”) was expressed relative to the required relative phase ($\phi_{req,j}$), that is, $\Delta\phi_j = \phi_j - \phi_{req,j}$, with $\phi_{req,j} = 0^\circ$ (in-phase) or $\phi_{req,j} = 180^\circ$ (antiphase). $SD\phi_j$ was used as an index of performance stability with low $SD\phi_j$ corresponding to a high degree of stability (cf. Schöner, Haken, & Kelso, 1986). A trial was excluded from further analysis if $|\bar{\phi}_{post} - \bar{\phi}_{pre}| > 360^\circ$ or if no stable pre- or post-switch behavior was established ($SD\phi_j > 30^\circ$; this criterion was based on the obtained frequency distribution of the $SD\phi_j$ values). In seven trials $SD\phi_{pre}$ or $SD\phi_{post}$ exceeded this criterion due to a brief change in ϕ_j of more than 270° . In these cases the performance measures were determined for five consecutive pre- or post-switch cycles that did not involve such a change. Finally, eight trials were excluded from further analysis. These trials were equally distributed over participants and conditions.

Switching Time

The main focus of this study concerned the transient stage of the bimanual behavior, that is, the coordination switch. To determine the behavioral measures during the switch, the switch region had to be defined first. To this end, the onset and end of the pattern change were determined following a procedure inspired by analyses performed by Byblow et al. (1994) and Wuyts et al. (1998). First, for the period of stimulus illumination, the point at which ϕ first deviated from $\bar{\phi}_{pre} \pm 2SD\phi_{pre}$ and the point at which ϕ first attained a value within the range of $\bar{\phi}_{post} \pm 2SD\phi_{post}$ were identified. These two points in time defined, respectively, the start and end of the period over which a linear regression line for ϕ was fitted. The intersections of this line with the values of $\bar{\phi}_{pre}$ and $\bar{\phi}_{post}$ were adopted as the exact onset (t_0) and end (t_{end}) of the switch, respectively. Switching time (τ_{sw}) was defined by $\tau_{sw} = t_{end} - t_0$. In addition, the values of τ_{sw} were normalized with respect to the pre-switch mean cycle duration (yielding τ_{sw}^*), to analyze switching time also in terms of the number of cycles (rather than time) needed for the switch.

Index of Coupling

To determine the relative contributions of the hands to the intended phase adjustment, an analysis similar to that developed by De Poel et al. (2005) for unintended transitions was applied. Detailed inspection of the trials revealed that although the two hands oscillated at identical frequencies, they did not always fully adhere to the required movement frequency as specified by the auditory pacing signal (see

also Results). As a consequence, the changes in phasing could not be determined reliably by simply comparing the movement phase of each individual hand to the phase prescribed by the pacing signal. Therefore, the evolutions of the individual phase angles (θ_L and θ_R , see Figure 1B) of the wrist movements were analyzed using the rate of change of θ (i.e., the phase velocity $\dot{\theta}$) as determined for the two hands, yielding $\dot{\theta}_L$ and $\dot{\theta}_R$ (see Figure 1C). Subsequently, for each hand, the mean value of $\dot{\theta}$ as obtained for the pre-switch period ($\bar{\dot{\theta}}_{\text{pre}}$) was subtracted from $\dot{\theta}$, thereby normalizing for the actual movement frequency. The amount of change in the phasing of the left hand (A_L) during the switching period (as illustrated by the dark gray areas in Figure 1C) was derived using

$$A_L = \int_{t_0}^{t_{\text{end}}} (\dot{\theta}_L - \bar{\dot{\theta}}_{L,\text{pre}}) dt \quad (1)$$

In the same fashion, A_R was calculated to determine the change in phasing of the right hand (cf. light gray areas in Figure 1C). The relative contribution of the left hand to the pattern change was expressed by the index of coupling (IC)¹:

$$IC = \frac{|A_L|}{|A_L| + |A_R|} \quad (2)$$

Thus, for each trial, IC (ranging from 0 to 1) revealed the degree to which the switch was mediated by adaptations in the phasing of either hand. For $IC = .5$ both hands contributed equally, whereas $IC > .5$ reflected larger adaptation in the phasing of the left hand ($|A_L| > |A_R|$) and $IC < .5$ reflected larger adaptation by the right hand ($|A_R| > |A_L|$). For each participant the values of IC thus obtained were averaged for each experimental condition.

Switch Pathway

For every trial the switch pathway was determined as being either “up” or “down,” corresponding to increasing or decreasing values of ϕ during the switch, respectively (cf. Kelso & Jeka, 1992). An “up” transition resulted from acceleration in the phasing of the left hand and/or deceleration of the right hand (i.e., $\dot{\theta}_L > \dot{\theta}_R$ within the switch period), whereas a “down” transition resulted from deceleration of the left hand and/or acceleration of the right hand (i.e., $\dot{\theta}_L < \dot{\theta}_R$ within the switch period). For each participant the percentage of “up” transitions was used for further analysis.

Statistical Analysis

The variables $\Delta\phi$ and $SD\phi$ were submitted to a repeated measures analysis of variance (ANOVA) with the between-participants factor handedness (LH, RH) and the

1. Note that $\text{mean}(\dot{\theta}_L - \bar{\dot{\theta}}_{L,\text{pre}})$ during the switch is equal to $\frac{1}{t_{\text{end}} - t_0} A_L$. Because the interval $t_{\text{end}} - t_0$ is equal for L and R, IC can also be defined as a relative measure of the average change in phase velocity of the two hands during the switch.

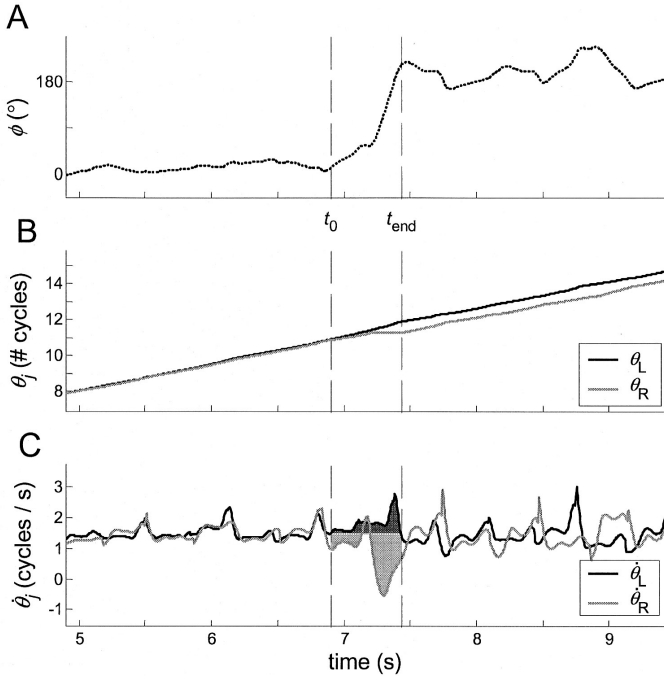


Figure 1—Illustration of successive steps in the derivation of *IC*, based on a single representative trial (movement frequency: 1.5 Hz) as obtained for a LH participant. Dashed vertical lines represent the moments of onset (t_0) and end (t_{end}) of the transition. A: Relative phase trajectory indicating a switch from in-phase to antiphase coordination. B: Unwrapped phase angles (θ , indexed by the number of elapsed cycles) for each hand around the switching period. C: Phase velocities $\dot{\theta}_L$ and $\dot{\theta}_R$ (L = left; R = right). Gray-shaded areas illustrate the amount of adjustment made by each arm: dark gray = left arm (A_L); light gray = right arm (A_R).

within-participants factors coordination mode (in-phase, antiphase), frequency (1, 1.25, 1.5, 1.75 Hz), and epoch (pre-, post-switch). IC , τ_{sw} , and τ_{sw}^* were submitted to a repeated measures ANOVA with the between-participants factor handedness (LH, RH) and the within-participants factors switch condition (in-phase to antiphase, antiphase to in-phase) and frequency (1, 1.25, 1.5, 1.75 Hz). In case the assumption of sphericity was violated, the degrees of freedom were adjusted using the Huynh–Feldt procedure. Besides significant effects ($p < .05$), tendencies towards significance ($p < .10$) were reported as well. In addition, the corresponding effect sizes (f) were calculated based on the partial eta squared (Cohen, 1988). Post hoc comparisons were based on a combination of paired-samples and independent-samples t -tests ($p < .05$). The latter were applied for all effects involving between-group comparisons.

In addition, the mean *IC* values obtained for the two handedness groups were compared to $IC = .5$ using one-sample t -tests. In this case, the effects sizes were calculated in terms of Cohen's d (Cohen, 1988).

Results

Pre- and Post-Switch Performance

Movement Frequency. During pre- and post-switch performance, the absolute difference in mean movement frequency between the left and the right arm never exceeded 0.08 Hz, which confirmed that in all trials the movements were 1:1 frequency-locked. In general, the prescribed frequencies were adequately performed, although three participants experienced some difficulties in locking their movements to the highest pacing frequency of 1.75 Hz. The interindividual averages and corresponding standard deviations were 1.01 Hz ($SD = 0.03$), 1.26 Hz ($SD = 0.06$), 1.51 Hz ($SD = 0.07$), and 1.74 Hz ($SD = 0.12$).

Phase Shift. Analysis of $\Delta\phi$ yielded a non-significant trend for handedness, $F(1, 11) = 3.65$, $p < .10$, $f = 0.26$, with mean $\Delta\phi = -4.9^\circ$ for RH participants (indicating right hand temporal lead) and mean $\Delta\phi = 0.7^\circ$ for the LH group. A significant Handedness \times Coordination Mode interaction, $F(1, 11) = 12.20$, $p < .01$, $f = 0.63$, further elucidated this tendency. Post hoc comparisons showed that for antiphase coordination LH participants (antiphase: mean $\Delta\phi = 3.0^\circ$; in-phase: mean $\Delta\phi = -1.6^\circ$) differed significantly from RH participants (antiphase: mean $\Delta\phi = -7.0^\circ$; in-phase: mean $\Delta\phi = -2.9^\circ$), and that for LH individuals the values were significantly higher for antiphase than for in-phase coordination. Furthermore, the significant main effect of frequency, $F(3, 33) = 4.73$, $p < .01$, $f = 0.31$, and subsequent post-hoc analyses showed that, on average, the values of $\Delta\phi$ became more negative with increasing frequency, indicating an increasing phase advance of the right hand (averaged over coordination modes and handedness groups; mean $\Delta\phi = -0.8^\circ$ [1 Hz]; -0.8° [1.25 Hz]; -3.2° [1.5 Hz]; and -4.5° [1.75 Hz]).

Relative Phase Variability. For $SD\phi$ the analysis revealed a significant main effect of coordination mode, $F(1, 11) = 201.01$, $p < .001$, $f = 3.04$, with antiphase (mean $SD\phi = 16.0^\circ$) being more variable than in-phase coordination (mean $SD\phi = 10.9^\circ$). The effect of frequency was also significant, $F(3, 33) = 6.10$, $p < .01$, $f = 0.39$. Post hoc tests demonstrated that over the three lowest frequencies $SD\phi$ decreased with increasing movement frequency (mean $SD\phi = 14.8^\circ$ [1 Hz]; 13.4° [1.25 Hz]; and 12.2° [1.5 Hz]), while performance at the highest frequency (1.75 Hz; mean $SD\phi = 13.2^\circ$) only differed significantly from performance at 1 Hz.

Switch Characteristics

Switching Time. Analysis of switching time (τ_{sw}) revealed no significant effects (mean $\tau_{sw} = 497$ ms; $SD = 85$ ms). When switching time was normalized to cycle duration (τ_{sw}^*), however, a significant effect of frequency was obtained, $F(2.2, 23.8) = 20.14$, $p < .001$, $f = 0.86$, which indicated that the proportion of a cycle that was used to switch from one coordination pattern to the other increased with movement frequency. Subsequent post hoc tests showed that all frequency conditions differed from one another. The mean values of τ_{sw}^* were 0.50 ($SD = 0.01$) of a cycle for 1 Hz; 0.61 ($SD = 0.17$) for 1.25 Hz; 0.73 ($SD = 0.14$) for 1.5 Hz; and 0.89 ($SD = 0.22$) for 1.75 Hz.

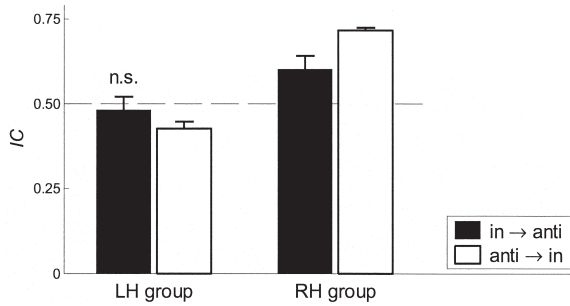


Figure 2—Mean values of IC as a function of handedness and switch condition. LH = left-handed group; RH = right-handed group. The dashed line indicates the value of IC corresponding to equal contributions of the left and right hand ($IC = .5$). All except one (indicated by n.s.) mean IC values differed significantly from $IC = .5$. For $IC > .5$ the switches were mainly mediated by the left hand; for $IC < .5$ they were mainly mediated by the right hand. Error bars represent the between-participant standard errors.

Index of Coupling. The mean IC was significantly higher for RH participants (.67) than for LH participants (.45; see also Figure 2), $F(1, 11) = 71.03$, $p < .001$, $f = 1.76$, indicating that the right-handers exhibited larger adaptations of the left hand during intentional pattern switching than the left-handers. Because $IC < .5$ implied larger adjustments by the right hand and $IC > .5$ implied larger adjustments by the left hand, the average values per group were subsequently tested against $IC = .5$ (one-sample t -tests). These t -tests revealed that the values of IC as obtained for the RH group were significantly higher than .5, $t(6) = 10.85$, $p < .001$, $d = 4.01$, whereas for the LH group a nonsignificant trend towards values lower than .5 was observed, $t(5) = -2.31$, $p < .10$, $d = 0.85$. In the LH group, 42% of the trials (between-participant $SD = 6\%$) were predominantly mediated by the left hand (i.e., $IC > 0.5$), whereas in the RH group this was the case for 74% of the trials (between-participant $SD = 9\%$). Hence, these results indicated that intentional switching predominantly involved phase adjustment in the movements of the nondominant hand, although this effect did not reach significance for the LH group.

The Handedness \times Switch Condition interaction was also significant, $F(1, 11) = 8.66$, $p < .05$, $f = 0.49$. Post hoc comparisons revealed that for RH participants the values of IC were significantly higher (indicating larger left-hand adaptations) when switching from antiphase to in-phase than when switching from in-phase to antiphase. In addition, Figure 2 suggests that switches from antiphase to in-phase coordination resulted in a larger difference in IC between LH and RH participants than switches in the reverse direction. One-sample t -tests of the average group values for each condition against $IC = .5$ revealed that for both the in-phase to antiphase switches, $t(6) = 2.93$, $p < .05$, $d = 1.11$, and the antiphase to in-phase switches, $t(6) = 23.64$, $p < .001$, $d = 8.94$, the IC values obtained for the RH group were significantly higher than .5, revealing that both switches were predominantly mediated by adaptations in the (nondominant) left hand. For the LH participants, however, only the antiphase to in-phase switches, $t(5) = -3.32$, $p < .05$, $d = 1.36$, resulted in a mean IC value that was significantly smaller than .5, indicating larger

adaptations in the (nondominant) right hand in this condition. The percentages of trials in which the left hand primarily mediated the switch were 38% for LH and 80% for RH participants when switching from antiphase to in-phase coordination, while for switches in the opposite direction less asymmetric distributions were obtained: 46% for LH and 67% for RH participants. Together, these results demonstrated that the predominance of phase adaptations in the nondominant hand during voluntary switches was more pronounced for switches from antiphase to in-phase coordination than for switches in the opposite direction.

In line with our predictions, the results indicated that, although in both groups the switches were primarily mediated by the nondominant hand, this effect was less pronounced in left-handers than in right-handers (cf. Figure 2). To test this difference between the handedness groups in a head-on fashion, we expressed IC in terms of the relative contribution of the *nondominant* (ND) hand to the switch (i.e., the numerator of Equation 2, A_L , was replaced by A_{ND}), yielding IC_{ND} . The repeated measures Handedness \times Switch Condition \times Frequency ANOVA performed on IC_{ND} revealed an effect of Handedness, $F(1, 11) = 21.41$, $p < .005$, $f = 0.88$, which indicated that the contribution of the nondominant hand was significantly larger in RH participants (mean $IC_{ND} = .67$) than in LH participants (mean $IC_{ND} = .55$). The effect of switch condition was also significant, $F(1, 11) = 8.66$, $p < .05$, $f = 0.49$. Note that the latter effect was identical to the Handedness \times Switch Condition interaction discussed in the previous paragraph.

Switch Pathway. Although for some participants individual preferences for a particular (“up” or “down”) switch pathway were observed, a combination of paired-samples and independent samples t -tests on the percentage of “up” switches revealed no significant effects: The switch pathways were distributed equally across groups and conditions.

Discussion

In the present experiment, we examined how intentional switches between rhythmic coordination patterns were mediated by phase adaptations in both hands in LH and RH participants. From the (both theoretically and empirically motivated) hypothesis of a handedness-related asymmetry in interlimb coupling strength, we predicted that the intentional switches in question were primarily mediated by adaptations in the movements of the nondominant hand. This effect was expected to be stronger in RH than in LH participants. In addition, we examined whether the previously reported reduction in switching time at higher movement frequencies was associated with an increased asymmetry in interlimb coupling strength. To examine these predictions, the degree to which the two hands altered their phasing during voluntary switches was determined and expressed in an interlimb coupling index (IC).

The first two predictions were clearly supported by the experimental results. For both LH and RH individuals the switches were predominantly mediated by adaptations in the nondominant hand. Although the asymmetry in the contributions of the two hands was relatively small (cf. Figure 2), the IC values revealed significant deviations from equal contributions of both hands (except for the switches from in-phase to antiphase coordination in the LH participants). This result is consistent with the proposed asymmetry in coupling strength and extends previous indications

of such an asymmetry during intentional switching in RH participants (Byblow et al., 2000; Carson et al., 1996). In addition, the present results underscored that coordination characteristics obtained for RH participants cannot always be smoothly generalized to LH individuals: Although in both groups the phase adjustments were mainly mediated by the nondominant hand, this effect was more pronounced in RH participants. As outlined at the beginning of this article, this difference between the handedness groups is in accordance with previous indications that left-handers are less consistent in their expression of handedness than right-handers (McManus et al., 1999; Peters & Servos, 1989; Shen & Franz, 2005) and indicates that in LH individuals the asymmetry in interlimb coupling strength is weaker than in RH individuals (cf. De Poel et al., 2005).

In correspondence with the findings of De Poel et al. (2005), no effects of handedness were observed with respect to the switch pathways, suggesting that the way in which the switches were mediated was governed by the asymmetric coupling between the hands rather than by the collective relative phase dynamics. Together, the present results indicated that the handedness-related asymmetry in interlimb coupling strength does not only determine the transient characteristics of spontaneous (unintended) phase adaptations (as revealed by De Poel et al., 2005), but also affects the way in which voluntary changes in interlimb coordination are effectuated. Interestingly, the asymmetry between the hands turned out to be larger for switches from antiphase to in-phase coordination (i.e., in the direction corresponding to spontaneous frequency-induced transitions) than for switches in the opposite direction, suggesting that either the asymmetry in coupling strength itself or the behavioral expression thereof was modulated by the intentional processes associated with the switch. Whereas in switching from anti-phase to in-phase coordination the system could exploit the intrinsic stability tendencies resulting from the interlimb coupling, these tendencies have to be opposed when switching in the reverse direction, which might call for the contribution of distinct dedicated processes (cf. Byblow et al., 1999, 2000; Carson et al., 1996), possibly mediated by the supplementary motor area (cf. Byblow et al., 1999).

Although the analysis of pre- and post-switch behavior revealed that the in-phase mode was performed more stably than the antiphase mode, the two switch conditions did not result in different switching times (τ_{sw} and τ_{sw}^*). As such, the current results do not support the general observation that switches to more stable patterns are performed more swiftly than those in the reverse direction (Byblow, et al. 2000; Carson et al. 1996; Serrien & Swinnen, 1999; Kelso et al., 1988; Scholz & Kelso, 1990). This deviant observation might be related to the fact that in the present study (unlike most previous studies) the pacing signal was present throughout the trial, to allow for adequate prescription of the different movement frequencies tested in the experiment. Possibly this pacing signal (consisting of two beeps per movement cycle) provided a perceptual anchor (e.g., Beek, Turvey, & Schmidt, 1992; Byblow et al., 1994), thereby diminishing the extent to which switching time was influenced by the difference in stability between the two patterns.² Still, the current detailed analysis of the relative contributions of the two hands (in terms of *IC*) revealed that

2. Note, however, that Carson et al. (1996) did observe a difference in switching time between the two switch conditions both in the absence and presence of an auditory pacing signal (one beep per movement cycle).

even in the absence of a difference in switching time, the way in which the switches were brought about depended on both handedness and switch condition.

The third prediction, regarding the effects of movement tempo, was not supported, given the absence of a frequency effect on the index of coupling (*IC*). At first blush, this difference between the current results and those obtained for unintended, relaxational transients (De Poel et al., 2005) might be interpreted as a consequence of the difference between the experimental tasks, involving intended vs. unintended transients, respectively. As argued above, (the expression of) the characteristic handedness-related asymmetry in coupling strength appears to be modulated by intentional processes (cf. Byblow et al., 1999, 2000; Carson et al., 1996). On this perspective, the present results might suggest that the influences of such processes increase with increasing frequency, thereby suppressing the intrinsic amplification of the asymmetry in coupling strength (as revealed by De Poel et al., 2005). This interpretation, however, should be treated with considerable caution, since specific methodological aspects of the experiment might also have affected the results in this regard.

In particular, it is conceivable that the frequency range tested in the experiment was not suitable to induce the expected effect of movement frequency. The stability of performance (as indexed by $SD\phi$) showed an optimum for the intermediate frequencies with, on average, variability being smallest for the 1.5 Hz frequency condition. This most stable frequency condition corresponded closely to the average preferred oscillation frequency for unimanual flexion-extension movements about the wrist (1.49 Hz) as determined by Peper and Beek (1998). The frequency-related amplification of the asymmetry in coupling strength observed by De Poel et al. (2005), however, was based on frequencies ranging from 1 to 1.5 Hz applied to lower arm movements, for which an average preferred frequency of 1.10 Hz has been reported (Beek, Rikkert, & Van Wieringen, 1996). Thus, it is possible that frequency-related changes in the asymmetry of interlimb coupling strength can only be observed when movement frequency is increased considerably beyond the preferred frequency of oscillation.

In contrast to the results of Carson et al. (1996) and Scholz and Kelso (1990), switching time τ_{sw} also remained unaffected by the manipulation of movement frequency. It is possible that the absence of an effect in this regard was associated with the fact that the frequency range applied in the experiment was centered around the preferred frequency of oscillation. An alternative explanation can be found in the presence of the pacing signal. As already mentioned in the preceding, such a signal may function as a perceptual anchor, thereby possibly affecting the way in which the switch is executed. However, the fact that the manipulation of movement frequency significantly affected τ_{sw}^* revealed that switching time was not characterized by a fixed perceptuo-motor anchoring strategy.

In sum, intentional switches between rhythmic coordination patterns were found to be primarily mediated by phase adaptations in the nondominant hand, and this effect was more pronounced for RH than for LH participants. These findings supported the conjecture that hand dominance is associated with an asymmetry in interlimb coupling strength (with the nondominant hand being more strongly influenced by the dominant hand than vice versa) and also indicated that intentional transient stages are (partly) governed by this asymmetry. In addition, the difference between the two switch conditions in this regard indicated that intentional

processes might weaken (the expression of) the handedness-related asymmetry in coupling strength.

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